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Ten-year variability and environmental controls of ecosystem water use efficiency in a rainfed maize cropland in Northeast China

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ABSTRACT

As a critical link between carbon and water cycles, water use efficiency (WUE) is an important metric for assessing ecosystem response to climate change. However, the controlling mechanism of WUE is still unclear because a number of environmental factors are usually cross-correlated in natural systems. Using the structural equation modeling (SEM) method, this study investigated the seasonal and inter-annual variations of WUE and their controlling mechanism based on 10 years of eddy covariance data in a rainfed maize cropland. The results showed that annual WUE varied between 2.1 g C $kg^{-1}H_2O$ and 3.6 g C $kg^{-1}H_2O$, with a multi-year mean of 2.8 g C $kg^{-1}H_2O$. At a daily timescale, leaf area index (LAI) was the primary controlling factor of WUE, while air temperature (Ta) and vapor pressure deficit (VPD) were both shown to have significant indirect effects on WUE through regulating LAI. Distinct controlling mechanisms of daily WUE were detected for years with different hydro-climatic conditions. The primary controlling factors were generally consistent in the 3 dry years (LAI, Ta and VPD). Moreover, WUE consistently showed negative response to soil water content in dry years, while an opposite response was found in wet years. Mean annual Ta was shown to explain 54% of the inter-annual variation of WUE. Despite the insignificant relationship between WUE and precipitation amount at an annual scale, the precipitation frequency was found to be a good predictor of the annual WUE. These findings provide important implications for the accurate simulation of ecosystem WUE, especially under drought conditions in semi-arid regions.

1. Introduction

Water use efficiency (WUE) is a critical metric that quantifies the trade-off between photosynthetic carbon assimilation and transpiration (Tr) at the leaf level (Farquhar et al., 1980). However, neither carbon assimilation nor transpiration can be observed directly at the ecosystem scale. The eddy covariance (EC) method can be used to estimate the gross primary productivity (GPP) and the evapotranspiration (ET) simultaneously (Baldocchi et al., 2001; Boese et al., 2017). Hence, ecosystem WUE is usually defined as the ratio of GPP to ET (Reichstein et al., 2002). As an important ecosystem property, WUE is the foundation of several popular ecosystem models (Morén et al., 2001; Tang et al., 2006; Van Wijk and Bouten, 2002). The successful application of these models relies on the ability to accurately estimate WUE. Therefore, comprehensive understanding of ecosystem WUE and its environmental controls may provide valuable implications on ecosystem responses to future climate change (Xue et al., 2015; Zhang et al., 2016).

Theoretically, any environmental factor influencing GPP or ET is supposed to affect WUE. The potential controlling factors of WUE included net radiation (Rn), air temperature (Ta), vapor pressure deficit (VPD), soil water content (SWC), leaf area index (LAI), and the ratio of diffuse to total radiation (Liu et al., 2015; Yang et al., 2010). However, previous studies, most of which were based on correlation or regression analysis (Xie et al., 2016a,b; Yu et al., 2008), often encountered difficulties in sorting out the controlling mechanisms of WUE because the multiple environmental factors are not independent of each other and often co-regulate ecosystem WUE (Niu et al., 2011). Some researchers have tried to reduce the cross-correlations among environmental factors by stratifying data into several groups; however, the thresholds for stratification were inevitably subjective, and the results were very difficult to interpret (Gao et al., 2017; Yang et al., 2010). Another

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confounding aspect is that, in addition to its direct effect, an environmental factor might impose an indirect effect on WUE through a mediation variable; e.g., drought has a direct effect on the plant physiology (e.g., stomatal conductance), which is manifested as the instantaneous reductions of both GPP and ET. Simultaneously, drought is also supposed to have a lagged effect on WUE by regulating the canopy structure and plant phenology, which could be roughly represented by a common ecosystem property, LAI (Reichstein et al., 2002). Fortunately, structural equation modeling (SEM) offers the potential to circumvent these limitations mentioned above. SEM has several advantages over traditional regression analysis; e.g., (1) it allows environmental variables to interact; (2) it provides a way to partition the net effect into direct and indirect effects; (3) instead of isolating a single controlling factor from others, SEM aims to systematically study the effects imposed by multi-factors in a holistic manner (Grace, 2006; Helman et al., 2017; Lamb, 2008). However, to our knowledge, there is no study reported using SEM to explore the environmental controls of WUE.

Moreover, climate projections have suggested that drought frequency and severity are very likely to be enhanced, with extreme weather events in northern mid-latitudes to be more frequent than in the past (Stocker, 2014). As a consequence, it is believed that WUE will increase under drought conditions due to a reduction in stomatal conductance, a widely accepted hypothesis at the leaf scale (Lu and Zhuang, 2010). However, with the increasing drought stress, ecosystem WUE has been reported to increase (Krishnan et al., 2006), decrease (Reichstein et al., 2002; Xie et al., 2016b), or increase under moderate drought conditions and then decrease under severe drought conditions (Gao et al., 2017; Lu and Zhuang, 2010; Reichstein et al., 2007; Yu et al., 2017). It is evident that previous studies concerning the drought effects on ecosystem WUE are still limited and controversial and are often based on short-term campaigns or modeling methods (Lu and Zhuang, 2010; Sebastian et al., 2013; Xie et al., 2016b; Yang et al., 2016; Yu et al., 2017).

This study aims to investigate the controlling mechanisms of ecosystem WUE using SEM, especially during drought conditions, based on 10 years (2005–2014) of eddy covariance flux data in a rainfed maize cropland in Northeast China. The specific objectives are (1) to analyze the seasonal variations of daily WUE and its environmental controls, (2) to compare the controlling mechanisms of daily WUE between years with different hydro-climatic conditions (dry and wet), (3) to explore the inter-annual variations of WUE and its relationship with environmental factors at the annual scale.

2. Materials and methods

2.1. Site description

This study was conducted at Jinzhou Agricultural Ecosystem Field Experiment Site (41°08′53″N, 121°12′06″E, 23 m a.s.l.), maintained by the Institute of Atmospheric Environment, China Meteorological Administration (CMA), Shenyang. The climate is characterized as temperate monsoons with warm, humid summers and dry, cold winters. The mean annual air temperature (1985–2014) is 10.1 °C, and the mean annual precipitation is 580.0 mm with nearly 70% occurring in summer (i.e., from June to August). The soil pH value is approximately 6.3, and the soil organic matter content ranges from 0.6% to 0.9%. Maize (rainfed) is usually sown in early May and harvested in late September. The planting density was around 5.1 plants per square meters. The growing season length is approximately 5 months (i.e., May to September). In the non-growing season, the surface is bare land. No-tillage or minimal tillage was adopted at this site. The soil is fertilized with 300 kg ha^{-1} $year^{-1}$ NH_4HCO_3 at the pre-seeding stage.

2.2. Fluxes, meteorological measurements and leaf area index

Fluxes of sensible heat (H), latent heat (LE), and CO_2 (net ecosystem exchange of CO_2, NEE) were measured using an Open Path Eddy Covariance (OPEC) system at 3.5 m above the ground, consisting of a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Inc., Logan, UT, USA), and an infrared gas analyzer (IRGA; LI-7500, LI-COR, Inc., Lincoln, NE, USA). The sonic anemometer measured the three components of wind speed and virtual temperature. The IRGA measured fluctuations of CO_2 and water vapor densities. Flux data were recorded at 10 Hz.

A meteorological tower was installed 30 m away from the EC tower. Photosynthetically active radiation (PAR) was measured with a quantum sensor (LI-190SB, LI-COR., Lincoln, NE, USA) at 4 m above the ground. Net radiation (Rn) was measured using a four-component net radiometer (CNR1, Kipp & Zonen, Corp., Delft, Holland) at 3.5 m above the ground. Two levels of air temperature (Ta) / relative humidity (RH, HMP45C, Vaisala, Helsinki, Finland) and wind speed (U, 014 A, Campbell Scientific Inc., UT, USA) were measured at 2.5 m and 4 m above the ground, respectively. Soil temperature (Ts, 107 L, Campbell Scientific Inc., UT, USA) at 6 depths (i.e., 0.05, 0.1, 0.15, 0.2, 0.4, and 0.8 m) and volumetric soil water content (SWC, CS616, Campbell Scientific Inc., UT, USA) measurements at 4 depths (i.e., 0.1, 0.2, 0.3, and 0.4 m) were installed close to the meteorological tower. Two soil heat plates (HFP01, Hukeflux Inc., Delft, Netherlands) were separately placed at 0.08 m below the soil surface. Precipitation was measured with a rain gauge (52203, RM Young Inc., Traverse City, MI, USA). All the meteorological data were recorded with a datalogger (CR23XTD, Campbell Scientific Inc., UT, USA), and then calculated as 30 min averages.

Since there was no diffuse radiation observation at the maize site, the clearness index (Kt) was used as a surrogate for the diffuse fraction of the total radiation (Gu et al., 1999). At a given solar elevation angle, a decrease in Kt generally indicates an increase in the diffuse fraction of total radiation.

Leaf area index (LAI, 8-day composited, 1 km) data from the MODIS C5 product were used. Data were downloaded from the Distributed Active Archive Center from the Oak Ridge National Laboratory (http://daacmodis.ornl.gov). According to the corresponding quality flags provided by the MODIS product, the bad-quality data, which was corrupted by heavy clouds, sensor malfunction, and other reasons, were discarded and then gap-filled using linear interpolation method to acquire a continuous daily LAI product.

2.3. Flux calculations and data processing

Half-hourly NEE, H, and LE were calculated and corrected using the EddyPro 6.0 program (LI-COR Inc., Lincoln, NE, USA). Double rotation was applied to set the 30-min mean vertical (w) and lateral (v) velocity components to zero. Correction for the density effect (WPL correction) was performed (Webb et al., 1980). The covariance maximization method was used to compensate for possible time lags caused by sensor separation. Corrections of both the low and high frequency components were applied to the flux data (Moncrieff et al., 1997, 2005). Data were excluded during periods with (1) incomplete half-hourly measurements; (2) rain events; (3) outliers (Papale et al., 2006) and (4) low turbulence conditions. A friction velocity (u^*) threshold was used as a cut-off, and nocturnal fluxes below the threshold were removed (Zhu et al., 2006). Flux data were then gap-filled using the marginal distribution sampling (MDS) method (Reichstein et al., 2005). Separation of net ecosystem exchange (NEE) into gross primary production (GPP) and ecosystem respiration (Re) was performed (Reichstein et al., 2005). Briefly, the daytime Re was estimated using the Lloyd & Taylor equation developed between the nighttime NEE and soil temperature every two weeks (Lloyd and Taylor, 1994). The GPP was then calculated as the difference between the modeled Re and measured NEE.

Data used in this study included measurements during 2005–2014. Ecosystem WUE (g C kg^{-1} H_2O) is calculated as the ratio of GPP to ET. ET was inferred from the measured LE. When analyzing environmental

controls of daily WUE, daily GPP and ET were calculated as daily sums of half-hourly values and only good quality data (i.e., the ratio of gap-filled to total half-hourly daytime data should be less than 50%) were used.

2.4. Structural equation modeling

The structural equation modeling (SEM) method was used to explore the controlling mechanisms of daily WUE. SEM is a multivariate statistical technique that has emerged as a synthesis of path analysis, factor analysis, and maximum-likelihood estimation. SEM can be used in either a confirmatory or exploratory mode (Grace, 2006). In a confirmatory mode, the model is specified based on a priori theoretical knowledge and then tested to determine whether the model adequately fits the data. In an exploratory mode, the initial theoretical model is adjusted based on the modification indices to improve the fit between model and data (Lamb, 2008). In this study, we first considered a full model that included all possible pathways, and then sequentially eliminated non-significant pathways (according to the *P* value) until we attained the final model. The χ^2 test of the model fit was used to determine whether the fit between model and data was adequate ($P >$ 0.05). The adjusted goodness of fit index (AGFI > 0.9), and root mean square error of approximation (RMSEA < 0.05) were also adopted as references to evaluate the fitness of the model (Grace, 2006). The significance test of the direct effect was readily acquired from the text output of the SEM. In addition, the significance tests of the indirect and total effects were conducted using a bootstrap method (Bollen and Stine, 1990).

A conceptual model (Fig. 1) was constructed based on the following knowledge from published studies. Rn, Ta, VPD, SWC, Kt, and LAI can influence WUE directly, and the abiotic factors (Rn, Ta, VPD, SWC, and Kt) can also influence WUE indirectly through their regulation on LAI (Tan et al., 2015; Yang et al., 2010). SEM analysis was executed using AMOS 21.0 (Amos Development Corporation, Chicago, IL, USA).

3. Results

3.1. Environmental factors

Fig. 2 shows the 10 year time series of environmental factors and WUE during 2005–2014. The mean annual Ta during the measurement campaign was 10.3 °C, which was slightly higher than the long-term mean (10.1 °C during 1985–2014) from a nearby weather station approximately 5 km away. The seasonal variation of Ta showed single-peak curves, with the lowest monthly value of -7.4 °C in January and highest monthly value of 24.7 °C in July. Rn showed seasonal variations similar to Ta but with larger day-to-day fluctuations, especially in the growing season. The highest daily mean Rn was 249.1 W m^{-2}, observed in July, 2009. The peak values of Rn usually occurred earlier (in late June or early July) than Ta (in late July or early August). The seasonal variation of VPD generally showed bimodal curves, with the first peak (in May) higher than the second one (in September) in each year. The highest VPD (2.6 kPa) was observed in late May, 2013. Clear seasonal and inter-annual variations were observed for LAI. The LAI peaks were generally observed in early to mid-July, corresponding to the transition period from the vegetative stage to the reproductive stage.

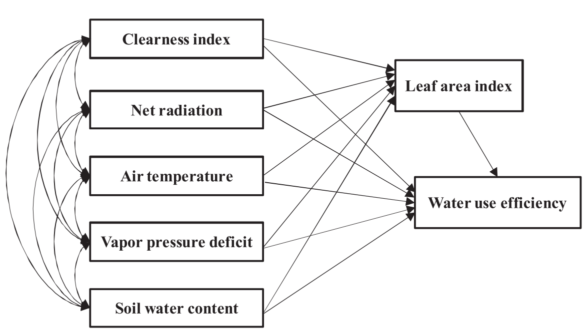

Fig. 1. Conceptual structural equation model of the relationships between WUE and environmental factors.
Note: Single-headed arrows represent causal relationships. Double-headed arrows represent cross-correlations.

Although mean annual precipitation during 2005–2014 (575.3 mm) was close to the long-term mean value (580.0 mm, 1985–2014), the inter-annual variation of annual precipitation was large, with the highest value observed in 2012 (869.2 mm, 50% higher than the long-term mean) and lowest value in 2014 (336.2 mm, 42% lower than the long-term mean). In addition, years 2009, 2011 and 2013 were also relatively dry in terms of annual precipitation, with 23%, 23% and 17% lower than the long-term mean, respectively. Corresponding to the seasonal distribution of precipitation, SWC showed distinct seasonal patterns over the 10 years. Of the 4 dry years classified by annual precipitation, mean annual SWC values in 2009, 2013 and 2014 were 31%, 15%, and 31% lower than the 10-year mean (2005–2014), respectively. By contrast, mean annual SWC in 2011 was 10% higher than the 10-year mean, despite the low precipitation received. Potential reasons for the mismatch between low precipitation and high SWC in 2011 might be as follows: (1) SWC might be influenced by the precipitation in the preceding year. The precipitation in 2010 was 40% higher than the long-term mean; (2) not only the amount but also seasonal distribution of precipitation could affect SWC. The year 2011 had a relatively uniform seasonal distribution of precipitation. More specifically, there were 48 days with precipitation events during the growing season in 2011, which was much higher than in 2009 (36 days) with a similar precipitation amount. Therefore, according to the SWC, precipitation and its seasonal distribution, the years 2009, 2013 and 2014 were classified as dry years. The other 7 years were simply classified as wet years since their annual precipitation and SWC were close to or higher than the long-term means.

3.2. WUE at the daily scale

3.2.1. Seasonal variations of WUE and its environmental controls

Seasonal variations of WUE generally showed parabolic curves, with several spikes mainly caused by extremely small ET values. The highest daily WUE was 25.7 g C $kg^{-1}H_2O$ in the late July in 2008. However, 95% of the daily WUE was less than 8.3 g C $kg^{-1}H_2O$ (Fig. 2).

All the data during 2005–2014 were pooled to examine the controlling mechanisms of daily WUE using SEM (Fig. 3). The adjusted SEM was shown to have a close fit to the data (χ^2 = 1.468, $P =$ 0.226, AGFI = 0.989, RMSEA = 0.021). Overall, this model explained 38% of the variation in WUE. The SEM results show that LAI had the largest direct positive effect (0.677) on WUE. Net radiation (Rn) had a direct negative effect (-0.330) on WUE but it was largely counterbalanced by an indirect positive effect (0.133) through its regulation on LAI (Table 1). The clearness index (Kt) also had a significant direct effect (0.185) on WUE. SWC had marginal but significant direct and indirect effects with opposite directions, resulting in a negligible total effect on WUE. In addition, VPD (-0.242) and Ta (0.435) had only indirect effects on WUE through modifying LAI, with higher WUE at higher Ta and lower VPD. Considering the direct and indirect effects together, it is clear that LAI was the primary controlling factor of WUE, followed by Ta, VPD, Rn, and Kt. SWC was not revealed as an important driver of daily WUE when all the 10 years of data were considered (Table 1).

3.2.2. Environmental controls on daily WUE between years with different hydro-climatic conditions

The SEM based on the 10 years of data (Fig. 3) explained a relatively low variance (38%) of the daily WUE, possibly because there are inter-annual variations in the soil nutrient status, leaf nitrogen content, management practices, crop variety, and so forth (Yang et al., 2010).

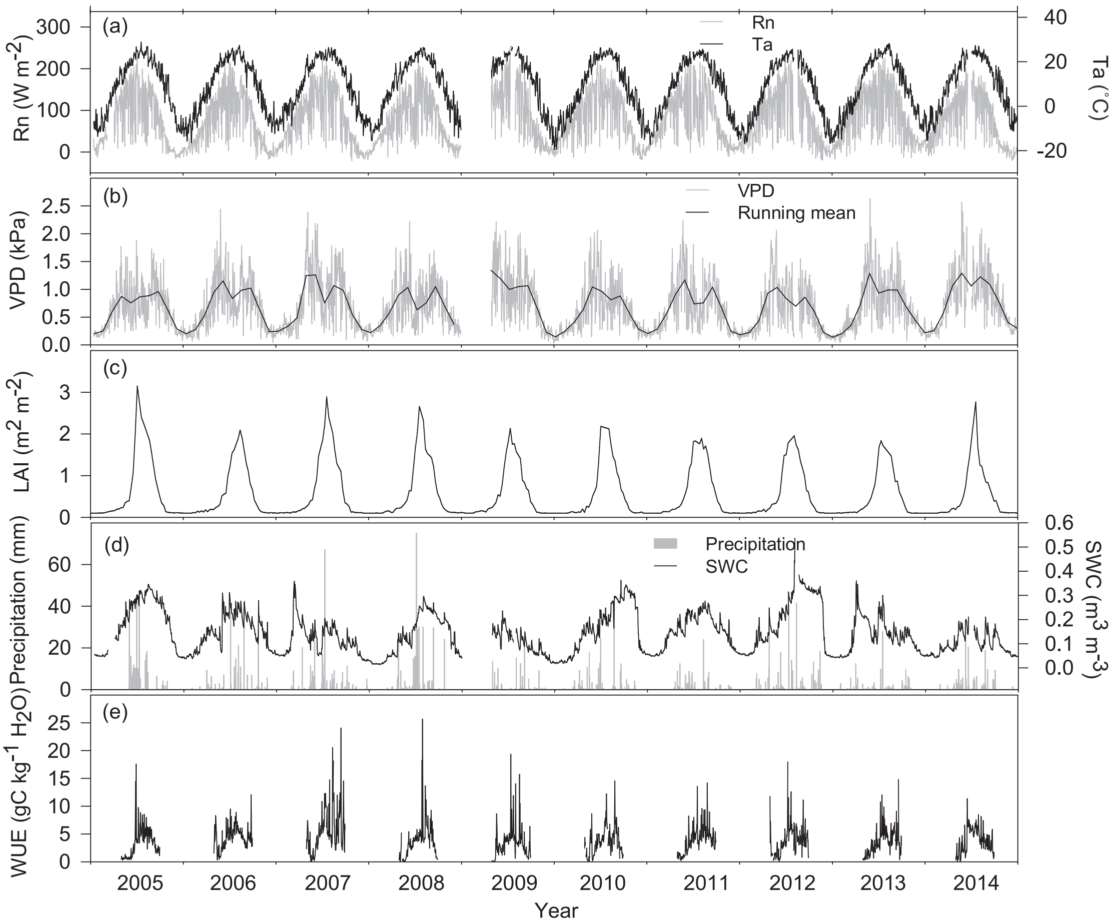

Fig. 2. Seasonal variations of (a) daily mean net radiation (Rn) and air temperature (Ta); (b) daily mean vapor pressure deficit (VPD); (c) daily leaf area index (LAI); (d) daily mean soil water content (SWC) and daily accumulated precipitation; (e) daily water use efficiency (WUE).

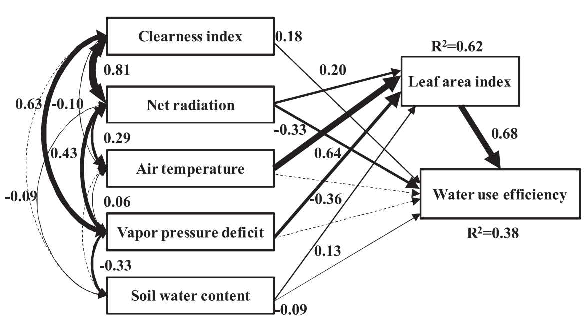

Fig. 3. Structural equation model for daily water use efficiency based on 10 years data.
Note: Non-significant paths are represented by dotted arrows. The thickness of the solid arrows reflects the magnitude of standardized path coefficients, and the numbers were also listed along with each path (no path coefficient was given for the non-significant path). R^2 values beside the response variables represent the variance explained by the environmental factors and the constructed relationships.

Another possible explanation might be that the controlling mechanisms were distinct between years with different hydro-climatic conditions. Thus, SEM analysis of environmental controls on WUE was conducted for each year separately to test this hypothesis. The controlling factors were sorted in descending order by the absolute value of their total effects on WUE (Table 2). The results show that the top three controlling factors of WUE were consistent in the 3 dry years, although with a different order of significance, i.e., Ta > LAI > VPD in 2009 and 2014, LAI > VPD > Ta in 2013. By contrast, there was no consistent pattern found for the primary controlling factors of WUE in wet years. Compared with the results in dry years, Rn, Kt and SWC were shown to have larger effects on WUE, while Ta and VPD were less important for WUE in wet years. In addition, SEMs based on data in each year generally explained more variance of WUE (38%～59%).

Table 1
Standardized direct, indirect, and total effects of environmental factors on daily WUE.

Environmental factors	Kt	Rn	SWC	VPD	Ta	LAI
Direct effect	**0.185**	**−0.330**	**−0.094**	−0.047	0.035	**0.677**
Indirect effect	0.000	**0.133**	**0.087**	**−0.242**	**0.435**	0.000
Total effect	**0.185**	**−0.198**	−0.007	**−0.288**	**0.470**	**0.677**

Note: values presented in bold represent the effects were significant ($P < 0.05$). Kt, clearness index; Rn, net radiation; SWC, soil water content; VPD, vapor pressure deficit; Ta, air temperature; LAI, leaf area index.

For the direct effect of the environmental factors on WUE (data not shown), the result was generally similar to the total effect shown above. A clear difference is that Rn was found to have a strong and significant direct effect on WUE in most of the years. This difference can be explained by the fact that Rn usually has a direct negative effect on WUE, and it was also found to have an indirect positive effect on WUE through modifying LAI. The opposite direct and indirect effects offset each other, resulting in a relatively weak negative total effect.

Table 2
Importance of environmental factors in descending order according to the absolute value of their total effects on water use efficiency (WUE).

Year	n	1st	2nd	3rd	4th	5th	6th	Explained variance of WUE
2005	48	--	--	--	--	--	--	--
2006	69	SWC	Rn	Ta	Kt	LAI	VPD	0.55
2007	125	LAI	Kt	Rn	VPD	Ta	SWC	0.40
2008	94	Kt	SWC	Rn	LAI	Ta	VPD	0.50
2009	91	Ta	LAI	VPD	Rn	Kt	SWC	0.39
2010	109	Ta	Kt	LAI	VPD	SWC	Rn	0.38
2011	115	LAI	SWC	Rn	Kt	VPD	Ta	0.59
2012	115	LAI	Ta	SWC	Rn	VPD	Kt	0.44
2013	143	LAI	VPD	Ta	SWC	Kt	Rn	0.50
2014	117	Ta	LAI	VPD	SWC	Kt	Rn	0.51

Note: "–" denotes that no valid values in 2005 due to the insufficient sample size. Variables in bold style represent their effects on WUE were significant. Kt, clearness index; Rn, net radiation; SWC, soil water content; VPD, vapor pressure deficit; Ta, air temperature; LAI, leaf area index. The shaded rows are dry years, and the others are wet years.

3.3. Annual WUE and its environmental controls

3.3.1. Inter-annual variation of WUE

Annual WUE varied between 2.1 g C $kg^{-1}H_2O$ (in 2005) and 3.6 g C $kg^{-1}H_2O$ (in 2007), with a multi-year mean of 2.8 g C $kg^{-1}H_2O$. There was no significant trend detected in annual WUE from 2005 to 2014. Annual WUE was closely related to monthly WUE in June and July, followed by WUE in May and September with lower correlations. WUE in August was not correlated to the annual WUE (Fig. 4).

3.3.2. Relationships between WUE and environmental factors at the annual scale

Regression analysis, rather than SEM, was conducted to explore the relationships between annual WUE and the environmental factors due to the limited sample size at the annual scale. The results showed that Ta was the primary controlling factor of annual WUE, explaining nearly 54% of the variation alone. In addition, annual WUE increased significantly with increasing VPD and decreasing SWC (Fig. 5).

4. Discussion

4.1. Environmental controls on daily WUE

In agreement with some recently published studies (Tan et al., 2015; Wagle et al., 2016; Xie et al., 2016b), the SEM Analysis based on all of the 10 years of data (n = 1024) showed that LAI, Ta, and VPD were important controlling factors of daily WUE at the Jinzhou site, with higher significance of LAI and Ta than VPD. This result is inconsistent with most of the previous studies suggesting that VPD was the most important controlling factor of WUE at the hourly and daily scales (Beer et al., 2009; Jia et al., 2016; Zhou et al., 2014, 2015). Potential reasons for this inconsistency are manifold. For instance, several researchers

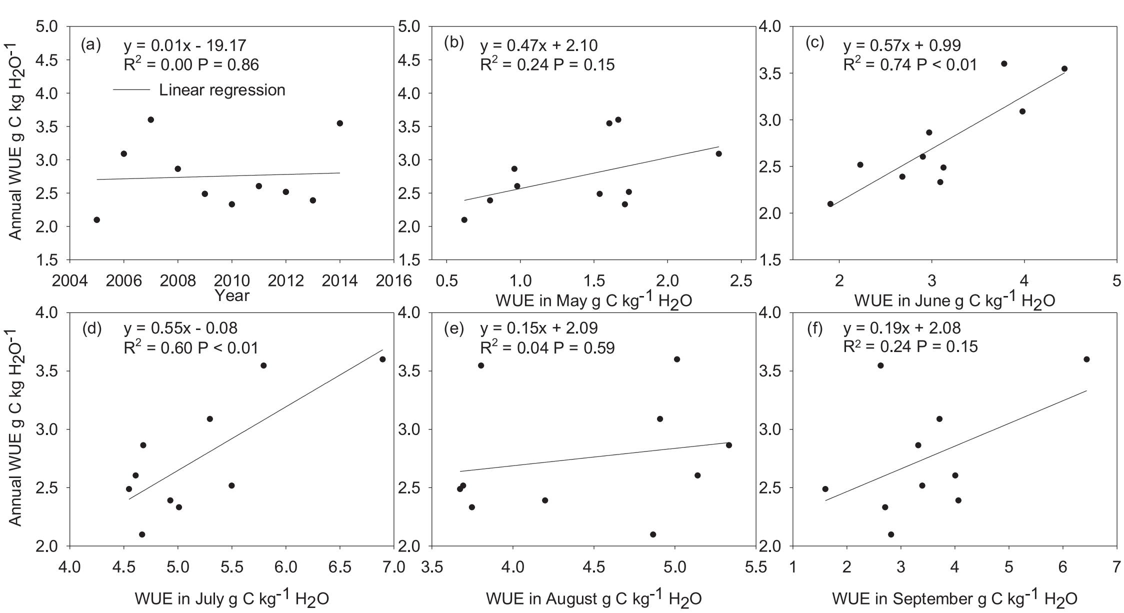

Fig. 4. (a) Inter-annual variation of water use efficiency (WUE) and its relationship with monthly WUE in (b) May (c) June (d) July (e) August (f) September.

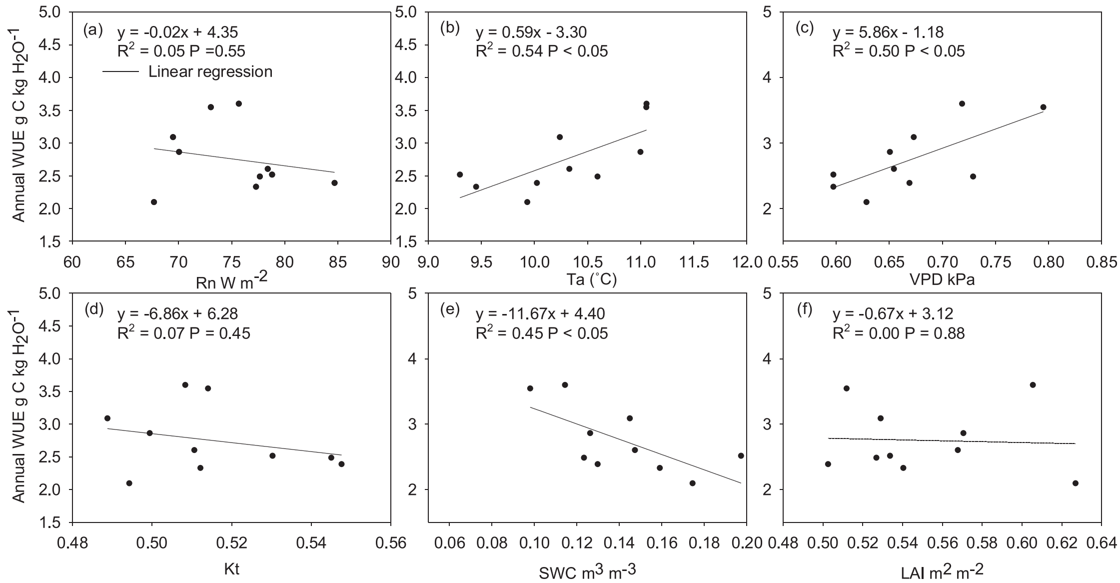

Fig. 5. Regression between annual water use efficiency (WUE) and mean annual (a) net radiation (Rn), (b) air temperature (Ta), (c) vapor pressure deficit (VPD), (d) clearness index (Kt), (e) soil water content (SWC), (f) leaf area index (LAI).

screened their data by excluding the early and late growing season to ensure that the ecosystem had a close canopy and stable LAI (Jia et al., 2016; Ponton et al., 2006). Similarly, some other studies were conducted in forest ecosystems with close canopies all the year round (Mahrt and Vickers, 2002; Morén et al., 2001). In those cases, LAI was nearly a constant and usually not considered as a controlling factor of seasonal WUE. Thus, the model based on the relationship between WUE and VPD was surely limited by its spatial and temporal applicability due to the data selecting and screening procedure when it was constructed (Xie et al., 2016a). However, a clear seasonal variation of LAI was often detected in agricultural ecosystems. In addition, the results of this study indicated that annual WUE was significantly related to monthly WUE in June and July (corresponding to the period with sharply increased LAI and open canopy), rather than WUE in August and September (corresponding to a close canopy); this result clearly highlighted the importance of the WUE in the early growing season for predicting annual WUE. Therefore, data covering the whole growing season were used to conduct the SEM analysis in this study. LAI was included as a mediation variable in SEM and was shown to be the primary controlling factor of WUE. The significant positive correlation between WUE and LAI might be due to its regulation on the ratio of transpiration to ET (Hu et al., 2008; Scott et al., 2015; Zhu et al., 2015).

Our results showed that Ta had a significant positive effect on WUE at the daily scale. This is similar to the results reported in some temperate ecosystems, but contrary to that in tropical and subtropical ecosystems (Tan et al., 2015; Zhu et al., 2014). The positive effect of Ta on WUE might be attributed to the positive correlation between Ta and LAI in temperate ecosystems (i.e., indirect effect in this study), which was clearly illustrated in Fig. 2 and Table 1. However, this was not the case in tropical ecosystems, in which LAI was mainly shaped by water-related variables (VPD and SWC) but not Ta. A possible explanation for the negative correlation between Ta and WUE in tropical ecosystems could be the disproportionate decreases in GPP and ET during low-temperature periods: the decrease in GPP is much less than that of ET (Tan et al., 2015).

It has long been recognized that VPD has a strong control over WUE at short timescales (Tan et al., 2015; Zhou et al., 2014). In this study, VPD was shown to have a negative effect on WUE, which is in accordance with most of the previous studies (Beer et al., 2009; Yang et al., 2010; Zhou et al., 2014). Similar to Ta, the total effect of VPD on WUE was mainly contributed by its indirect effect through LAI.

As an important driving factor for both photosynthesis and ET, Rn received much less attention than other environmental factors in previous studies. A recently published study revealed that introducing a radiation related intercept term in the classic WUE model considerably improved the model performance (Boese et al., 2017), which implied that radiation might be important in controlling WUE. In this study, the SEM analysis based on 10 years of data shows that Rn had only a marginal total effect on WUE. However, the partitioning of the total effect suggested that Rn had a strong, negative direct effect on WUE, and it was largely offset by a smaller, indirect positive effect. Therefore, our result supports the view that the radiation plays an important role in regulating WUE, and it should be considered in future WUE models.

4.2. Response of WUE to drought

There is a prolonged debate on the response of WUE to soil water content (Gao et al., 2017; Huang et al., 2017; Xie et al., 2016a,b; Yang et al., 2010). A widely accepted explanation is that the relationship between WUE and SWC was undoubtedly subject to influences of other factors; e.g., WUE was found to decrease with soil water potential at high levels of VPD and increase with soil water potential at low levels of VPD in an Ozark forest (Yang et al., 2010). Due to the ubiquitous cross-correlations among environmental factors, it is difficult to isolate a single controlling factor from others when its influence on WUE is discussed. Instead, SEM is designed to study the simultaneous effects of multiple environmental factors in a holistic manner. The SEM results based on the 10 years of data showed that the total effect of SWC on WUE was insignificant because the direct and indirect effects were similar in magnitude but opposite in direction, although SWC has been believed to be an important controlling factor of WUE (Table 1). Thus, the drought effect on WUE was further explored to evaluate the response of WUE to SWC in each year. Interestingly, we found that the total effect of SWC was negative in all the dry years (2009, 2013 and 2014) and positive in all the wet years. More specifically, both the direct and indirect effects in dry years were negative, except only an insignificant indirect effect in 2013, while both the direct and indirect effects in wet years were positive, except only an insignificant direct effect in 2007. In dry years, the direct effect of SWC on WUE was higher in its absolute value than the indirect effect (Table 3). This result implies that SWC tended to influence WUE directly and negatively in dry years, rather than indirectly through shaping LAI. It is in accordance

Table 3
Direct, indirect, and total effects of soil water content (SWC) on daily water use efficiency (WUE) in each year.

Year	n	Direct effect	Indirect effect	Total effect
2005	48	–	–	–
2006	69	**0.425**	0.047	**0.473**
2007	125	−0.072	0.083	0.011
2008	94	0.211	**0.213**	**0.423**
2009	91	−0.074	−0.05	−0.123
2010	109	0.053	0.071	0.124
2011	115	0.149	**0.341**	**0.490**
2012	115	0.076	**0.302**	**0.378**
2013	143	**−0.305**	0.048	**−0.257**
2014	117	**−0.142**	**−0.068**	**−0.210**

Note: values presented in bold style represent the effects were significant ($P < 0.05$); "–" denotes that no valid values in 2005 due to the insufficient sample size.

with the expected response of WUE at the leaf level, to reduce the water consumption while maintaining a relatively high photosynthesis rate (Farquhar et al., 1980). By contrast, it appears that SWC was more likely to have an indirect effect on WUE in wet years. For example, a much higher contribution of indirect effect than direct effect was found in both 2011 and 2012. A possible explanation might be that the maize ecosystem was rarely influenced by drought events due to the favorable water conditions in wet years, thus SWC mainly imposed its positive effects on WUE indirectly through its regulation on LAI. The contrasting responses of WUE to drought between different hydro-climatic conditions were also reported in an urban forest ecosystem (Xie et al., 2016b).

4.3. Inter-annual variation of WUE

Mean annual WUE during 2005–2014 was 2.8 g C $kg^{-1}H_2O$ in this study, close to the values reported in two maize sites (irrigated and rainfed, both of 3.2 g C $kg^{-1}H_2O$) in North America (Suyker and Verma, 2010) and a maize site (2.9 g C $kg^{-1}H_2O$) in Southeast Asia (Alberto et al., 2013), and larger than the WUE of the maize cropland (0.87 g C $kg^{-1}H_2O$) in Northwestern China (Tang et al., 2017). The very low WUE in Northwestern China was probably caused by the extremely arid conditions (annual precipitation of only 126.7 mm) and the relatively low canopy height (1.8 m).

There was no significant temporal trend detected in annual WUE from 2005 to 2014. The correlations between GPP, ET and WUE at annual scale were analyzed. As expected, annual WUE was shown to be positively correlated with GPP, but negatively correlated with ET. In addition, the inter-annual variation of WUE was more ascribed to GPP than ET. This is consistent with most results reported by previous studies (Hu et al., 2008; Yang et al., 2016).

To the best of our knowledge, there are few studies focused on the controlling mechanisms of the inter-annual variation of WUE in the past, perhaps due to the limited time duration of datasets. Regression analysis showed that the annual WUE was closely related to mean annual Ta in this study. In addition, it is worth noting that WUE had a significant positive relationship with VPD at the annual scale, which is clearly different from the negative relationship found between these two variables at the daily scale. Since the negative relationship at the daily scale was based on a solid method (SEM) and extensively reported (Beer et al., 2009; Jia et al., 2016; Zhou et al., 2014, 2015), the positive relationship between WUE and VPD at the annual scale might be caused by the strong cross-correlation between Ta and VPD. It has also been reported that VPD was a poor determinant of WUE at growing season and annual time scales in an oak-dominated temperate forest (Xie et al., 2016a).

Despite many findings that annual precipitation is a good predictor of inter-annual variations in ecosystem productivity (Huxman et al., 2004; Jongen et al., 2011; Niu et al., 2011; Scott et al., 2015) and ET (Biederman et al., 2016; Helman et al., 2017), WUE was not significantly related to annual precipitation in this study ($R^2 = 0.204$, $P = 0.19$, data not shown). However, the precipitation frequency (i.e., number of precipitation days) during the growing season was found to have a significant and negative relationship with annual WUE ($R^2 = 0.52$, $P < 0.01$). This result strongly emphasized the importance of the seasonal distribution of precipitation on WUE at the annual scale (Jia et al., 2016; Jongen et al., 2011; Liu et al., 2016; Zhou et al., 2013).

5. Conclusion

In this study, seasonal and inter-annual variations of WUE and their controlling mechanisms were analyzed using SEM method. The SEM analysis based on 10 years of data showed that LAI, Ta, and VPD were important controlling factors of daily WUE. When SEM was performed separately for each year, it was found that the controlling mechanisms were different for dry and wet years. The primary controlling factors were consistent in the 3 dry years (Ta, LAI, and VPD). By contrast, the primary controlling factors in wet years were inconsistent. Response of WUE to SWC was also different between dry and wet years. WUE consistently showed negative responses to SWC in dry years, but positive responses in wet years.

Annual WUE ranged from 2.1 g C $kg^{-1}H_2O$ (in 2005) to 3.6 g C $kg^{-1}H_2O$ (in 2007), with a multi-year mean of 2.8 g C $kg^{-1}H_2O$. Inter-annual variation of WUE was mainly ascribed to GPP. Regression analysis showed that Ta was the most important controlling factor of annual WUE, explaining nearly 54% of the variation alone. Despite the insignificant relationship between WUE and annual precipitation amount, precipitation frequency was found to be a good predictor of annual WUE ($R^2 = 0.54$, $P < 0.01$).

These findings have several important implications for future studies of WUE. First, the SEM method should be extensively employed in exploring the complex ecosystem responses to cross-correlated environmental factors. In this study, the cross-correlations among the environmental factors were fully considered in the SEM. Simultaneously, the net effects of environmental factors were easily separated into direct and indirect effects. It was found that a lack of significant relationship using regression analysis doesn't necessarily mean the environmental factor was not important, and it might be a result of the cancelling result of its strong but opposite direct and indirect effects. Second, our results showed that LAI, rather than VPD, was the primary controlling factor at the rainfed maize cropland. Data selection might restrict the applicability of a constructed model based on the relationship between WUE and VPD. Finally, the 10-year measurement period covers episodes from extremely high to low annual precipitation at this site. The long-term data provided us a great opportunity for comprehensively analyzing the effects of extreme events on WUE. Therefore, solid SEM analysis based on long-term observations is strongly recommended for an in-depth understanding of WUE controlling mechanisms in the future.

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